Short note

Sexuality of *Dysoxylum spectabile* (Meliaceae)

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Abstract

Some individuals of the endemic New Zealand tree *Dysoxylum spectabile* (Meliaceae) have female flowers (pollen lacking), while others have flowers that act principally as males (ovules reduced in number and size). Three natural populations of mature trees in the Auckland region have strongly male-biased sex ratios.

Keywords: sexuality - floral morphology - sex ratio - *Dysoxylum* - Meliaceae.

Introduction

Dysoxylum spectabile (Forst.f.) Hook.f., hereafter referred to by its Maori name kohekohe, is endemic to New Zealand and is the southernmost representative of the predominantly tropical family Meliaceae. Kohekohe is widely distributed in coastal and lowland forests between the North Cape and the northern part of the South Island. Although conspicuous when flowering because of its cauliflorous habit, the floral dimorphism of this tree has only recently been established (Braggins *et al*. 1999).

Those authors described kohekohe as having two kinds of flowers, borne on separate individuals: female flowers, whose anthers look well-formed but contain no pollen (and do not open), and "male/hermaphrodite" flowers, with functional anthers and ovules that seldom mature into seeds.

The cryptic nature of this dimorphism is paralleled by recent discoveries in two other familiar New Zealand trees: *Corynocarpus laevigatus* (Corynocarpaceae), found to be gynodioecious (Garnock-Jones *et al*. 2007), and *Toronia toru* (Proteaceae), found to be dioecious (Gardner 2008).

This article criticizes some of the details given by Braggins *et al*. (1999) for kohekohe, particularly with respect to the sex ratio of natural populations. Note that because the "male/hermaphrodite flowers" seldom set seed they and the trees bearing them will be referred to simply as males.

Materials and Methods

Since 2005 I have made observations on kohekohe trees in the Auckland region. The species is commonly cultivated in the older parks here, such as Cornwall Park (but Outhwaite Park's several old trees may be survivors from, or descendants of, the original volcanic "rock-forest" trees). Natural populations with numerous mature individuals, as well as a good representation of younger ones, can be found in a number of Auckland's coastal forest reserves. Three of these populations were studied, at Sylvan Park (Takapuna), Dingle Dell (St Heliers), and Kepa Road (Orakei). Voucher specimens were not made.

Observations

Flowering

The flowering of kohekohe begins in early winter (in Auckland, late May) and lasts about a month. In a good flowering year the creamy-white to greenish flowers appear in their thousands on the branches and trunks (Figure 1). They are nectariferous and have a honey-like scent. Common day-time visitors in the Auckland mainland region are the tui bird (*Prosthemadera novaezelandiae*) and honey-bees and bumble-bees. In other parts of the country, the bellbird (*Anthornis melaneura*) is likely to be a major pollinator (e.g., on the Poor Knights Is., personal observation).

The sex of a kohekohe tree can be determined not just during flowering but also for some time subsequently. This is because male flowers are soon shed from the ageing inflorescence, and the bare inflorescence axis then falls from the tree in the next several weeks. By contrast, female flowers persist on the inflorescence axis, shedding only their perianth, stamen-tube and style as they age (Figure 2). A female inflorescence may stay in this state on the tree for two months or more. (However, by the time the fruits have ripened all unfertilized flowers have been shed).

Figure 1. *D. spectabile*. Male tree (Cornwall Park, at Manukau Road), mid-June 2007, showing profuse cauliflorous flowering. Inflorescences are c. 20 cm long.

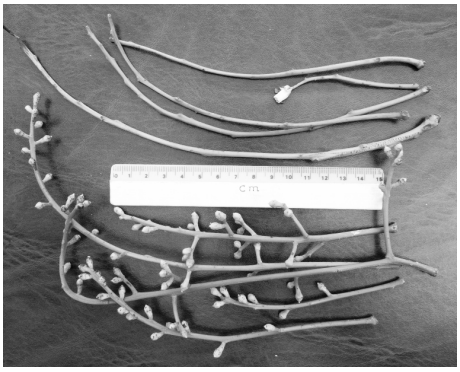

Figure 2. *D. spectabile* inflorescences, post-flowering. Males (above), females (below). One male inflorescence bears a last, terminal flower. Scale is 15 cm long.

Figure 3. *D. spectabile* flowers. Male (left), female (right). Longitudinal section, perianth mostly removed. Note the similar-sized ovaries. Scale bar is 1 cm long.

The cryptic nature of the floral dimorphism is shown in Figure 3. Also see the illustrations of Braggins *et al.* (1999), especially those showing the anthers and stigmas of the two flower types.

My observations are in agreement with these authors' finding that male flowers tend to have a staminal tube that is slightly longer and narrower than those of the females. The difference is insufficiently large or constant though for reliable discrimination of gender (Figure 4).

Braggins *et al.* (1999) state that male flowers generally lack ovules. This is contrary to my experience, which is that the ovaries of male flowers usually have 2 ovules in each of their 3 locules. I have never seen them with empty locules or aborted ovules. The ovaries of female flowers differ only in being slightly larger and in sometimes being 4-locular.

The stigma of the male flower appears identical to that of the female (see Braggins *et al.* 1991, figures 7, 8), and the pollen, which is usually liberated before the flower opens, often reaches the receptive sticky latero-ventral part of the stigma just a millimetre or so away.

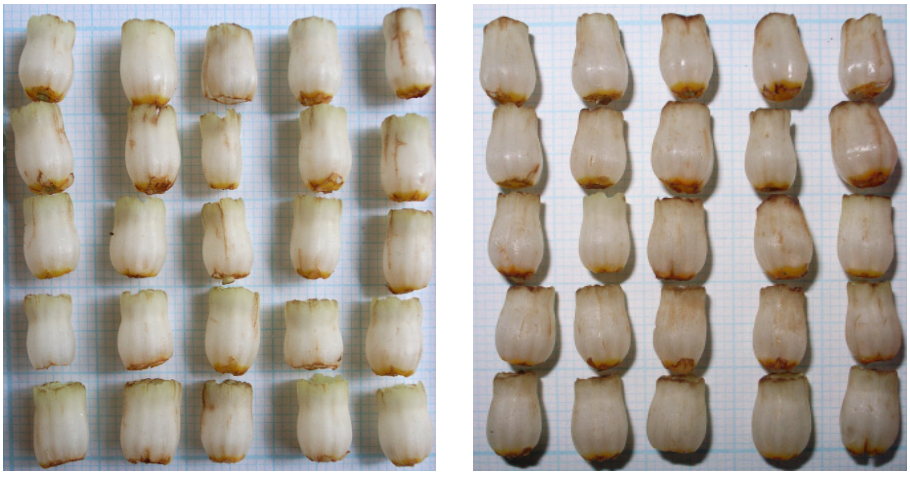

Figure 4. *D. spectabile*, detached stamen tubes. Males (left), female (right). Tubes of each sex are c. 1 cm long.

Sex ratio

The kohekohe population at Sylvan Park was closely observed in June 2006. Flowering was profuse that year. There were very few trees in this notable pre-European forest remnant (Gardner 1986) that did not bear inflorescences on the burrs of their trunks and branches. This sampling found 58 trees to be male and 17 female. All males here were examined and all were found to be fully ovuliferous.

Flowering of the Dingle Dell and Kepa Road trees was observed in June 2008. At both places a fair number of trees were not flowering at all, or bore so few flowers (and in their crowns rather than on their trunks) that none could be sexed. At Dingle Dell, a ratio of 30 male trees to 0 females was obtained. At Kepa Road, the ratio was 25 males to 6 females.

Flowering of the seven old trees at Outhwaite Park (Grafton) was observed in June of 2006, 2007 and 2008. The sex ratio here was 5 males to 2 females. In the 2008 flowering, a relatively poor year, the two female trees were rather less floriferous than the males.

Casual observations were made on all these populations in late summer, at about the time of fruit ripeness. Male trees bore hardly any fruit, up to a maximum of c. 20 per tree but often fewer. The male tree illustrated in Figure 1 was re-examined in November 2008 – of the hundreds of flowers shown in Figure 1 only four had set fruit. In contrast, well-grown female trees typically produce several hundred infructescences, each of which may bear up to c. 5 or more fruits.

Discussion

The sex ratio information presented here, particularly that from Sylvan Park in 2006, suggests there is a strong bias towards males in the Auckland region. Re-examination of the Dingle Dell and Kepa Road populations in a good flowering year is desirable, but it is my impression that trees "resting" (that is, remaining vegetative) at these sites in the 2008 flowering season were not especially numerous.

Braggins *et al.* (1999) found a predominance of males in NZ herbarium material (flowering specimens: 39 males to 7 females). This contrasted with the "40% to 50%" ratio (raw data not given) they found in their three natural populations (two from Auckland, one from Wellington). They attempted to explain the discrepancy by reference to a greater amount of flowers borne by male trees, which would make them more attractive to collectors. I suggest the contrary, that it is their "40% to 50%" ratio which requires explanation. Since they refer to having some difficulty physically accessing the flowers of their populations, perhaps their result is just due to faulty sampling.

Godley (1964, 1979) recorded male bias in more than a dozen dioecious NZ species (principally trees or shrubs). He suggested that an increased proportion of males raises the efficiency of pollination/fertilisation in such plants. It is intuitive that optimal physical spacing for an outcrossing species might resemble a close-packing arrangement of a larger number of males around a lesser number of females. It is hard though to see how this group-selectionist argument could be transformed into one of individual advantage, beginning from the 1:1 sex ratio that simple sex-determining systems generally give (and which is selected for under the requirement that in the population as a whole there be equality of investment into maleness and femaleness).

Alternatively, it has been suggested that "female load", the supposed greater cost a female incurs in reproducing, is responsible for the male-biased ratios (e.g., Webb & Lloyd 1980). In my opinion, the lack of anecdotal evidence for this concept in some well-studied groups (such as forestry trees), as well as the ability of females to adjust their fruit-bearing "burden" from year to year through abortion or by resting for a season, militate against thinking "female load" is widely applicable to tree species.

It was pointed out by an anonymous referee of this article that resting by females could result in male-biased ratios, and this is certainly a possible interpretation of the Dingle Dell and Kepa Road results. But I think it would be surprising if synchronicity of resting by males has not been selected for, at least in wind-pollinated species. In animal-pollinated ones, production of male flowers in the season(s) of poor female flowering could "tide over" the local population of pollinators, and conceivably might advantage particular male individuals or subpopulations.

The simplest explanation for the very low level of fruit set by male flowers would be that some considerable degree of self-sterility is present, as the "female-sterile" component of a dioecious breeding system. Some botanists, however, might consider kohekohe to be gynodioecious. They would term what I have called males, hermaphrodites, and explain the low fruit set by reference to some as yet unknown detail of the pollination process. Or, they might suggest, for example, that females are producing their abundance of fruit apomictically. A discovery of abundantly fruiting "male/hermaphrodite" trees would stimulate a closer examination of pollination physiology here.

Gender variation and the sex ratio of natural populations are fundamental parts of a species' biology and should be desiderata for the next generation of Flora-writers. Such studies though require long-term commitment. In kohekohe, for example, the ability of male trees to produce seed gives the opportunity for pollination experiments that will show which sex is the heterogametic one. But the growing-up of the progeny to sexual maturity might take twenty years or more.

Similarly, the testing of hypotheses about how the sexes might differ in vigour, longevity, tendency to rest for a season, etc., might most readily be done in a long-term plantation experiment, since the age of wild kohekohe trees is not easily determined, the wood having indistinct growth-rings.

Acknowledgements

This note is dedicated to the memory of J. A. (Jack) Rattenbury 1908-2008, whose advice and insight on such matters I miss.

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